FOSSILS OF THE MILWAUKEE FORMATION:

A DIVERSE MIDDLE DEVONIAN BIOTA FROM WISCONSIN, USA

Kenneth C. Gass, Joanne Kluessendorf, Donald G. Mikulic
and Carlton E. Brett

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DISCLAIMER: This book is a general guide to fossils of the Milwaukee Formation and not an extensive manual for health and safety when visiting this site. Furthermore, because potential hazards may change over time, prior to undertaking any fossil collecting activities, you need to make yourself aware of any RISKS, DANGERS, HAZARDS and LEGAL IMPLICATIONS associated with visiting and collecting fossils at any particular site. The publisher, authors or any associated parties cannot be held responsible for your failure to do so, nor any consequences thereof.

Printed and bound in the UK

In Memory of
Dr. Joanne Kluessendorf
(1949–2018)

Joanne Kluessendorf with cast of *Dunkleosteus*; December, 2017.
Courtesy of Beth A. Johnson and The Geological Society of America.

Preface

Over one hundred years have passed since H.F. Cleland wrote *The Fossils and Stratigraphy of the Middle Devonic of Wisconsin* (1911) — the first and only volume written largely on the Milwaukee Formation biota. Typical of similar works of its day, its illustrations were mostly black and white drawings. During the last century, new material has been gathered, many additional species have come to light, much has been learned, and advances in technology have made it possible to economically publish books having many full color photographs. Today around 250 species, subspecies, unnamed species and ichnospecies have been identified from the Milwaukee Formation, nearly 180 of which are illustrated in this book. These are represented by new and old material, including type and figured specimens wherever practical. Moreover, the large collections from this diverse biota have enabled a wide variety of fossil studies that depend on large sample sizes. It is our hope that this compilation of information and photographs will enlighten and entertain regional fossil collectors, spark the interest of researchers and budding paleontologists, and reach the hands of graduate students and professionals studying Devonian paleontology and others seeking fertile grounds on which to base their research, as offered in this much-neglected but diverse Middle Devonian biota.

Each major taxon of the biota is covered in its own chapter. Each of those chapters includes a discussion of that taxon and in most cases photographs of representative Milwaukee Formation fossils labeled to show important observable morphological features. The chapter then presents photographs of many of the species identified within that major taxon. The names of the other species of that taxon known to exist in this formation but not shown are listed. Terms that are introduced but not defined in the text are defined in the Glossary. Sections on stratigraphy, Milwaukee's cement industry, paleoenvironments, modes of life, organism interactions, taphonomy, fossil collecting in the Milwaukee Formation, preparation methods, and major collections round out the discussion.

Whenever known, the collectors of the fossils shown are indicated with their initials in the figure captions. The identities of those collectors are as follows: Benedict Bagrowski (BB), Elmer Dahlman (ED), Ira Edwards (IE), Marlene O. Emielity (MOE), Damien K. Gass (DKG), Jeanette L. Gass (JLG), Joshua S. Gass (JSG), Kenneth C. Gass (KCG), Kevin M. Gass (KMG), Lauri A. Gass (LAG), Todd C. Gass (TCG), Thomas A. Greene (TAG), Spence Havlick (SH), Thomas James (TJ), Ronald Kneusel (RK), Thomas Maier (TM), Donald G. Mikulic (DGM), Milwaukee Cement Company (MCC), Charles E. Monroe (CEM), Gilbert O. Raasch (GOR), Jeannette E. Roberts (JER), H. Rollins (HR), Lindsey V. Stenerson (LVS), Karly S. Tellekson (KST), Edgar E. Teller (EET), and Stanley Wisniewski (SW). The collectors of the specimens residing in the Greene Geological Museum were typically not recorded in the museum catalogs, but were either Thomas A. Greene, various Milwaukee Cement Company workers, or others.

Classification, descriptions and morphological terminology for invertebrates generally follow the current editions of the appropriate volumes and parts of the *Treatise on Invertebrate Paleontology*. *Fishes of the World, Fifth Edition* (Nelson et al., 2016) was similarly an indispensable resource for fishes. The generic placement of many species has been updated based on the most recently published studies and consultation with various specialists. Identifications should be considered tentative and targets for future investigation. Due to the tentative nature of the identifications, diagnoses are not given.

Prefixes of specimen numbers given in the figure captions indicate the respective repositories, as follows: MPM=Milwaukee Public Museum; UWM-GM=Greene Geological Museum, University of Wisconsin—Milwaukee; V or PAL=National Museum of Natural History, Washington, D.C.; VPF=Museum of Comparative Zoology, Harvard University; WESM=Weis Earth Science Museum, Menasha, Wisconsin. The prefix XXX-KCG indicates that the specimen resides at the indicated museum, but the catalog number is that given by KCG and not by the museum. Higher taxonomic placement of the species shown in each photograph, typically order and family, are stated in the corresponding figure caption (e.g., Arthrodiriformes:

Dunkleosteidae). If the figure caption does not state where the fossil was found, the specimen was collected either at one of the quarries near the Milwaukee River in northeastern Milwaukee County (mainly those operated by the Milwaukee Cement Company), or from Estabrook or Lincoln Park. Unless otherwise indicated, the photographic work was that of KCG.

KCG, DGM and JK are indebted to the late Joseph G. Emielity, Katherine G. Nelson, and Gilbert O. Raasch—each being curators of Milwaukee Formation fossils—for their friendship, for sharing their wealth of knowledge, and for solidifying our interest in this subject. Richard Fortey is thanked for reviewing a draft of the manuscript, especially the introductory and arthropod chapters, and providing useful input. We thank the following for reading drafts of the section on the indicated group of organisms and/or examining photographs of that group and providing valuable input: Robert K. Carr (fishes); Brian Chatterton and James Cook (trilobites); Jed Day (brachiopods); Andrej Ernst (bryozoans); Paul Kenrick (land plants); David Loydell (graptolites); George McIntosh (blastoids); Colin Sumrall (edrioasteroids); Heyo Van Iten (conulariids); Olev Vinn (tentaculitoids); and Brian Witzke (crinoids). A special thank you goes to Patricia Coorough-Burke for open access to the material at the Milwaukee Public Museum and providing much information and support. We are indebted to Stephen Dornbos and his staff (Greene Geological Museum) and the late Joanne Kluessendorf (Weis Earth Science Museum) for access to the collections in their respective museums and accommodating our needs. Amanda Millhouse and Kathy Hollis (National Museum of Natural History) and Jessica Cundiff (Museum of Comparative Zoology) are thanked for photographing material in their respective museums. Linda Deith (The Wisconsin Geological and Natural History Survey), Emma MacPherson (Canadian Society of Petroleum Geologists), and Beth A. Johnson are thanked for permission to use the indicated published images. Robert K. Carr, Terry C. Grande, and Joanne Kluessendorf are thanked for allowing us to publish figures based on their drawings. Lisa Marine (Wisconsin Historical Society), Jennifer Pahl (Milwaukee Public Library), and Susan Peschel (American Geographical Society Library, University of Wisconsin-Milwaukee Libraries) are thanked for providing scans of images and other materials in their care. JK and DGM thank the Wisconsin Historical Society for use of their archives. We also thank Denise Baker for help with Word issues; Richard Bizley for painting the cover image; David Bradbury for helping locate specimens; David Comfort for preparing certain fossils; Niles Eldredge, Gerald Kloc, and Bruce Lieberman for helpful discussions on phacopid systematics; Curt Klug for years of collecting trips with DGM and JK; Todd Gass for providing hardware and software support and for helping process some of the images; Ron Kneusel for suggesting that the book be written; J. Maisey for verifying the identity of the shark fin spine; and Dietmer Schumacher for providing conodont preparation methods and permission to use his published images. Finally, we thank David Penney of Siri Scientific Press for extending the opportunity to publish this work and for making improvements.

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Chapter 4 — Taphonomy

The Milwaukee Formation exhibits a wide range of fossilization modes that help us recognize the rich diversity of its fossil biota. Together, these modes are capable of preserving not only hard parts, but some unmineralized ones and traces as well. Additionally, depending on the mode of fossilization, features of both the outside and inside surfaces of shells can be preserved in detail.

The life in Milwaukee's Devonian seas was undoubtedly subject to the same kinds of post-mortem processes encountered by organisms in today's shallow, warm seas. These processes begin after death of organisms or after parts of skeletons are discarded, such as the molted exoskeletons of arthropods. Soft parts are rapidly degraded and lost by bacterial and chemical decomposition, or serve as a meal for scavengers. Skeletal hard parts are also subject to breakdown by processes that include disarticulation, fracturing, abrasion, and chemical dissolution. The effects of these processes vary somewhat with temperature, pH, salinity, currents, and other factors, but these are significantly reduced once the carcass becomes buried. For optimal preservation, it is therefore important that burial takes place as soon as possible after death.

While the rate of burial and other factors in play during deposition of the Milwaukee Formation were in most cases not sufficient to preserve soft tissues, conditions were often favorable for fossilization of shells, bones, plant remains, and other mineralized and unmineralized skeletal materials.

Skeletal Minerals and Preservation

The dominant minerals or organic materials in the skeletal remains of most of the biota that frequently fossilize in the Milwaukee Formation can be classified into the following categories.

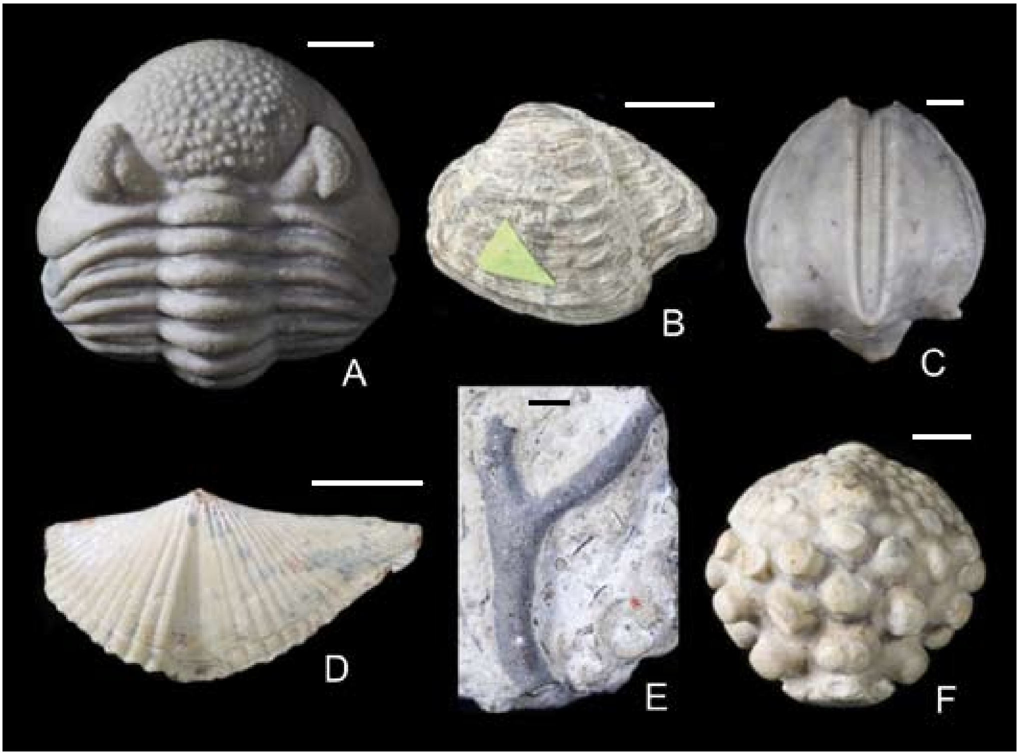
Calcite and Aragonite

The most common polymorph of calcium carbonate, calcite is the main constituent of the hard parts of echinoderms, corals, bryozoans, craniiform and rhynchonelliform brachiopods, microconchids, and trilobites that abound in the Devonian Milwaukee (Fig. 6) and other Paleozoic units. The resulting permineralized fossil is relatively hard and durable as well, regardless of what mineral crystallized within its pores. The skeletal pieces of echinoderms including the Milwaukee Formation's crinoids, blastoids and edrioasteroids, consist of porous single crystals of calcite.

The calcareous shells of most organisms also include aragonite, which is another polymorph of calcium carbonate; these include most mollusks and modern corals. Due to its unstable nature, few Devonian fossils contain any aragonite. Most of the Devonian aragonite has transformed to calcite or dissolved. Aragonitic skeletons tend to undergo early dissolution and to be preserved as molds.

Fig. 6 (top, opposite). Calcareous skeletal materials; Lindwurm Member. **A:** The trilobite *Eldredgeops? norwoodensis* (Stumm, 1953); WESM-KCG 1126; scale bar 5mm. **B:** The bivalve *Palaeoneilo persinnuata* Pohl, 1929; MPM 13757; scale bar 5mm. **C:** Calyx of the blastoid *Pentremitidea* sp.; WESM-KCG 890; scale bar 2mm. **D:** The brachiopod *Orthospirifer clelandi* (Griesemer, 1965); MPM 16580; scale bar 1cm. **E:** The bryozoan *Eridotrypa appressa* (Ulrich, 1890); UWM-GM 5880; scale bar 5mm. **F:** Calyx of the crinoid *Melocrinites subglobosus* (Weller, 1898); WESM-KCG 19; scale bar 5mm.

Fig. 7 (bottom, opposite). Apatitic skeletal materials fossilized by permineralization. **A:** The conulariid *Conularia milwaukeensis* Cleland, 1911; MPM P28134; scale bar 5mm. **B:** Tooth of the sarcopterygian fish *Onychodus* sp.; MPM 477; scale bar 2mm. **C:** Fin spine of the placoderm fish *Eczematolepis telleri* (Eastman, 1898); MPM 470; scale bar 1cm. **D:** The lingulid brachiopod *Orbiculoidea telleri* Cleland, 1911; MPM P28142; scale bar 5mm. **E:** The lingulid brachiopod *Barroisella? rectilatera* (Hall, 1859); MPM 5136; scale bar 5mm. **F:** Tooth plate from a ptyctodont placoderm fish; UWM-GM 10259; scale bar 5mm.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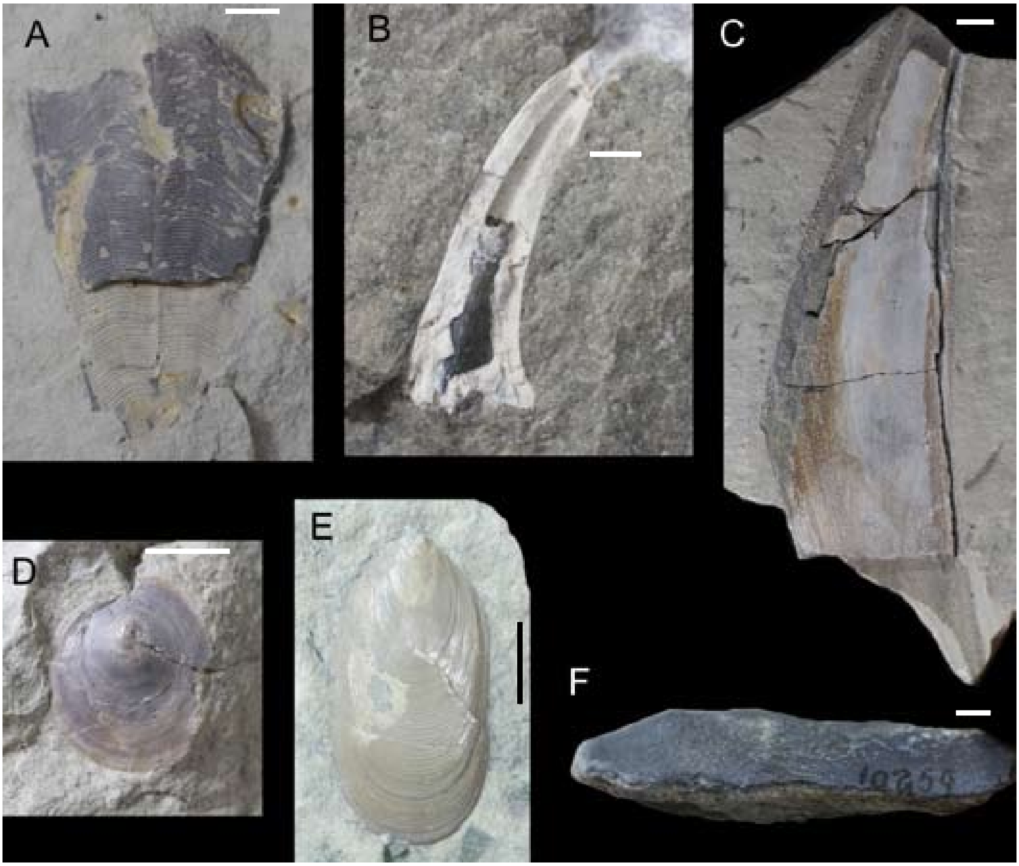
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Apatite

The conodonts, conulariids, and linguliform brachiopods of the Milwaukee Formation all contained forms of the phosphatic mineral, apatite. The same is true of the fishes, including the teeth of sarcopterygians and sharks, and the plates, spines, and teeth of placoderms. That apatite persisted after permineralization, imparting an appearance and composition that stand in sharp contrast with that of the surrounding matrix. The colors of these fossils are usually shades of pink, purple, white, black, or amber (Fig. 7). Phosphatic skeletal material of the fish in the Milwaukee Formation is so distinctive in appearance that even small fragments are usually enough to distinguish them from all other fossil taxa.

Chitin and Other Organic Materials

The skeletal materials of some organisms lack significant amounts of the previously mentioned minerals, instead consisting mostly of chitin, cellulose or other organic materials. In the Milwaukee Formation, this includes fungi, plant fossils, chitinozoans, phyllocarids, scolecodonts, graptolites, and placoderm scales. As with animals that contain apatite, the color of fossils with organic skeletal remains tends to make them stand out clearly from the surrounding matrix (Fig. 8). Plant fossils, fungi and graptolites tend to be dark gray to black due to their high carbon content. Some of the plant and fungus fossils of the Milwaukee Formation are partially composed of coal (Fig. 9).

Modes of Alteration of Skeletons

Once the organism is buried, the slow process of fossilization can begin. Skeletons are commonly altered in various ways depending upon their original compostions and their tendency to decay, dissolve or have their pores infilled. Common modes of alteration include permineralization, replacement, cabonization, and formation of internal and external molds.

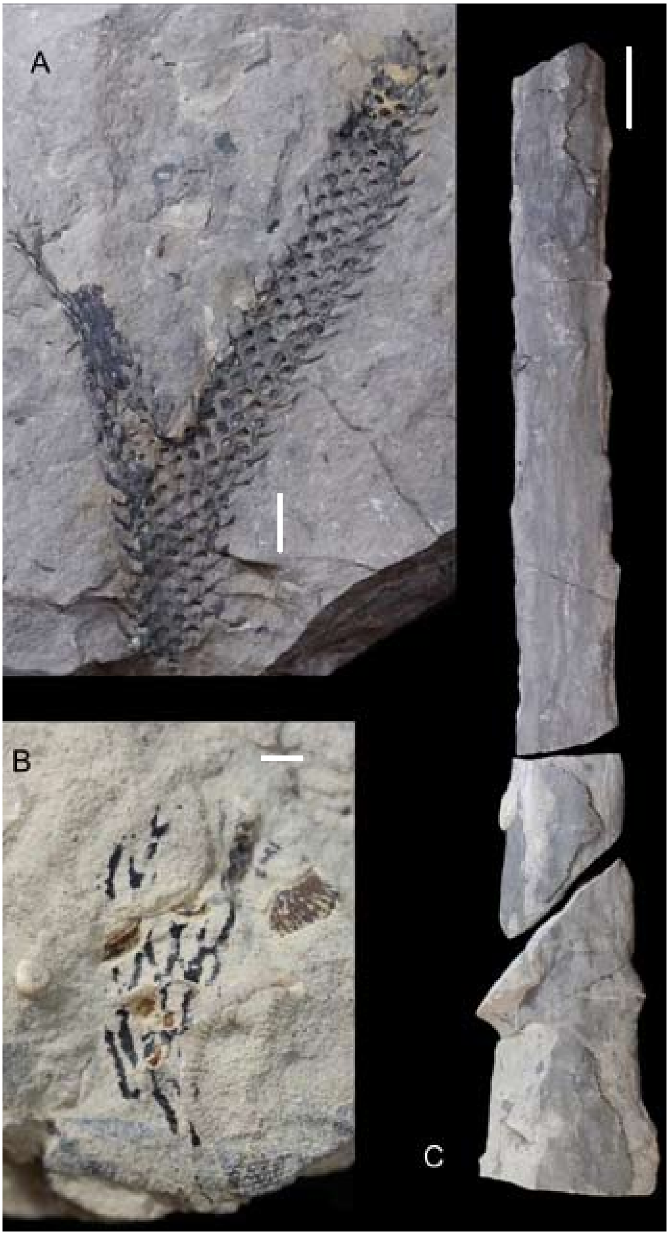

Fig. 8. Organic remains fossilized by permineralization. **A:** Axis (branch) of a lycopod; UWM-GM 9768; scale bar 1cm. **B:** The dendroid graptolite *Callograptus* sp.; MPM P28130; scale bar 2mm. **C:** The arborescent fungus *Prototaxites milwaukeensis* (Penhallow, 1908); MPM 402; scale bar 5cm.

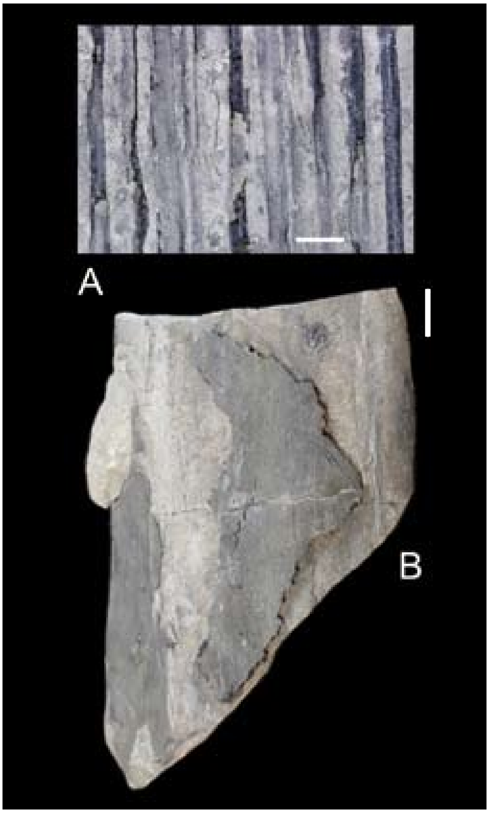

Fig. 9. Fossils of terrestrial organisms partially coalified; Berthelet Member. **A:** Bark from a cladoxylopsid? trunk; UWM-GM 25808; scale bar 1cm. **B:** Piece of the arborescent fungus shown in the previous figure; note the outer layer of coal; scale bar 2cm.

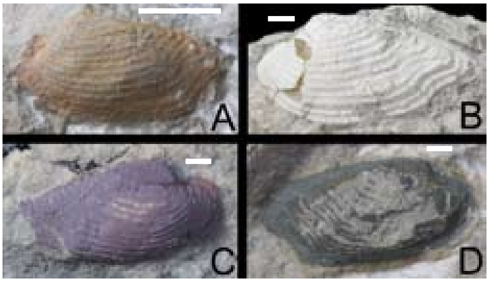

Fig. 10. Valves of the bivalve *Palaeoneilo corrugata* Pohl, 1929, fossilized by replacement by various materials. The valves shown in A, C, and D were presumably replaced by marcasite and certain impurities that then weathered to produce oxidized materials of various colors. The valve shown in B was replaced by silica. **A:** Left valve; MPM 13579; scale bar 5mm. **B:** A silicified left valve; MPM 466; scale bar 2mm. **C:** Right valve; MPM 468; 2mm. **D:** Right valve; MPM 13546; scale bar 2mm.

Permineralization

One fossilization mode found in the Milwaukee Formation, particularly the Lindwurm Member, is permineralization, in which calcite, or to a lesser extent dolomite, silica or other dissolved minerals in the groundwater crystallize within the pores of the remains. This is particularly typical of porous skeletons such as those of echinoderms. The resulting composition of the fossil is therefore a combination of the organism's chemistry (which is quite varied in a biota as diverse as that of the Milwaukee Formation) plus that of the externally derived minerals that crystallized within the organism's remains. This mixture of materials, aided by the effects of post-fossilization chemical changes and weathering processes, helps explain the many variations in colors and physical/chemical properties of the fossils within this formation. The body fossils of most lithified skeletal remains are typically permineralized to some degree (Figs. 6–9).

Replacement

Some fossils in the Milwaukee Formation were preserved by replacement, whereby sediment pore water-derived minerals entirely replaced the skeletal materials. This is most conspicuously observed where marcasite, pyrite or silica are the invading minerals. Replacement by marcasite is common in this formation. Many of those fossils are powdery in texture, and of a variety of colors, due to the weathering of marcasite to ferrous sulfate and the introduction of other mineral impurities. In the North Point Member, many of the shells are silicified, with the silica being in the form of white chert (Fig. 10).

Carbonization

This alteration mode, typically occurring in organisms that lack mineralized skeletons, results when the organic materials are reduced mainly to carbon, and is marked by the characteristic black color of the fossil (Figs. 8 & 9).

Internal / External Molds

Many of the fossils in the Milwaukee Formation, especially the Berthelet Member, are in the form of internal and external molds (Fig. 11). These are formed when a shell surrounded by consolidated sediment is dissolved by groundwater or weathered away after the object is buried, thus leaving a gap showing where the shell had been. The layer of rock that surrounds the outside surface of the shell shows the impression of external features known as the external mold. It therefore shows, in reverse, the shell's external dimensions and surface features such as ornamentation. The sediment that filled the concave inside surface of the shell shows, also in inverted relief, the shell's interior dimensions and such structures as muscle scars. The thickness of the shell can be derived by measuring the gap between the internal and external mold. In many cases, the fossil started as a replacement composed of marcasite, but then became molds once the marcasite had altered to ferrous sulfate, which then either dissolved or weathered away. An interesting feature of the internal and external molds of the Berthelet Member is that they generally have a thin, pigmented coating or staining on their surfaces. This generally imparts a charcoal gray or orange coloring, but other colors and shades are common (Fig. 12).

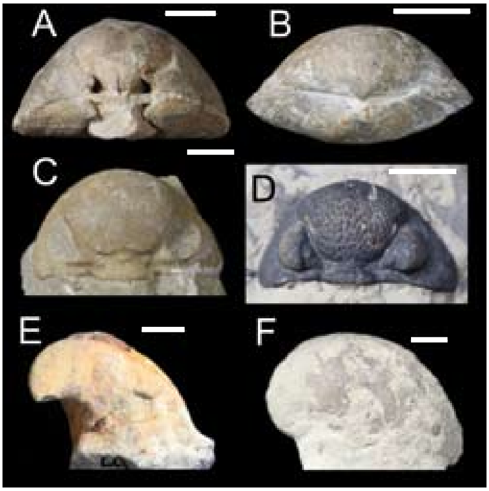

Fig. 11. Internal molds of shells of three types of animals (left), each compared with permineralized shells of the same or similar species (right). Notice that, in contrast to the permineralized equivalent fossils, the internal molds lack tubercles and other surface details, but may include structures indicating the location of features on the interior of the shell. **A:** The brachiopod *Schizophoria iowensis musculosa* Griesemer, 1965; MPM 15232; Berthelet Member; scale bar 1cm. **B:** *Schizophoria iowensis musculosa* Griesemer, 1965; MPM 16435; Lindwurm Member; scale bar 5mm. **C:** The trilobite *Eldredgeops? norwoodensis* (Stumm, 1953); MPM P26724; Berthelet Member; scale bar 5mm; glacial drift; Doctor's Park, Fox Point, Milwaukee County. **D:** *Eldredgeops? norwoodensis* (Stumm, 1953); scale bar 2mm. **E:** The gastropod *Platyceras?* sp.; MPM P28195; scale bar 5mm. **F:** *Platyceras?* sp.; MPM P28131; scale bar 5mm.

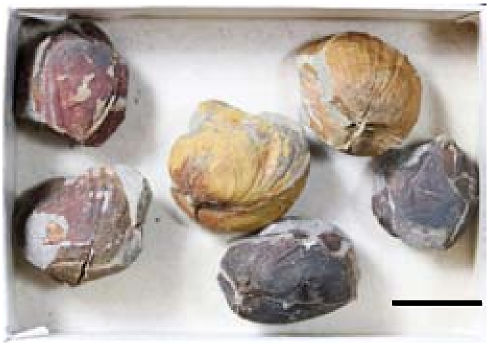

Fig. 12. Internal molds of the brachiopod *Eumetabolotoechia greeni* (Cleland, 1911), all recovered from the same small slab. The thin mineral coating on the surfaces of these fossils is more colorful than that of the typical molds from the Berthelet Member. MPM-KCG uncatalogued; scale bar 1cm.

Cavity Formation and Geodization

This occurs in cases where very rapid burial entombed shells of organisms with soft parts intact. After the soft, interior tissues of three-dimensional animal carcasses have decomposed, and if the space they occupied is not filled by sediment, the skeletal remains are essentially hollow. This provides a cavity into which fluids with dissolved minerals, such as calcite, can enter during or after lithification and crystalize on the cavity walls, as occurred often in the Milwaukee Formation. If the invading mineral is calcite, the result is a calcite geode. This was a common process occurring within brachiopods (Fig. 13), bivalves, and crinoid calyces. If massive bryozoans and corals were hollowed by dissolution, they also were targets of geodization. Other dissolved minerals, such as sphalerite (Fig. 14), pyrite (Fig. 15) and millerite (Fig. 16), commonly crystalized within these cavities as well, generally in the center of the void after calcite has crystallized around the margins of the cavities.

In the dolomitic upper layers of the Berthelet Member, these cavities (also known as vugs) may instead be coated or filled with a sticky, black, tar-like substance derived from organic remains that seeped into the cavities from the overlying strata (Fig. 17). The resulting asphaltum vugs are frequently found within partially hollowed cephalopods of this member. Asphaltum also coats the surfaces of some fossil molds (Fig. 18).

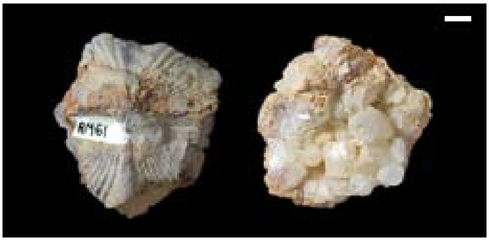

Fig. 13. Two views of a geodized brachiopod filled with calcite; MPM P28132; Lindwurm Member; collected by KCG; scale bar 5mm.

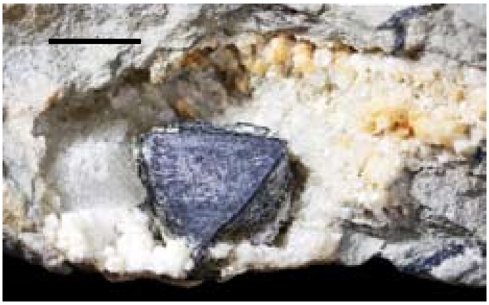

Fig. 14. Geodized brachiopod with a single octahedral crystal of sphalerite (zinc sulfate) and calcite lining; MPM P28133; Lindwurm Member; collected by KCG; scale bar 5mm.

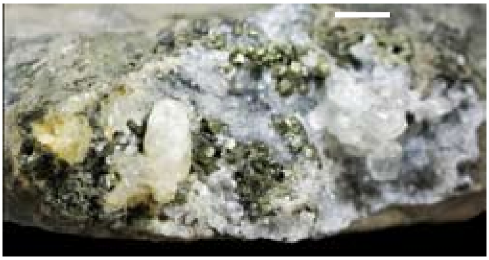

Fig. 15. Crystals of pyrite and calcite in a partially cavitated cephalopod; UWM-GM 32967; Berthelet Member; scale bar 1cm.

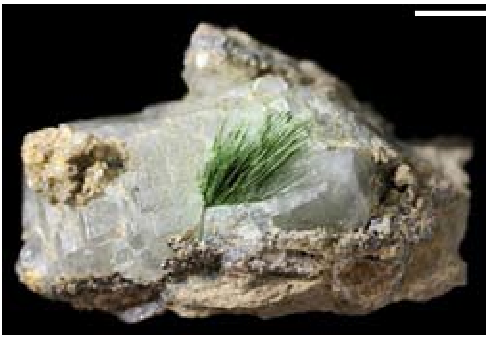

Fig. 16. Millerite (nickel sulfide) secondarily altered on its surface to emerald green zaratite (hydrous nickel carbonate) and calcite in a cavitated bryozoan; MPM Mi 20590; probably Berthelet Member; collected by KCG; scale bar 5mm.

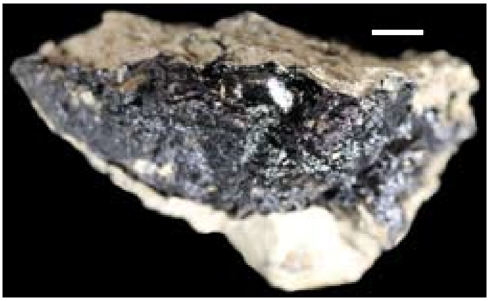

Fig. 17. Asphaltum in an unidentified cavity; MPM Mi 20591; Berthelet Member; collected by KCG; scale bar 5mm.

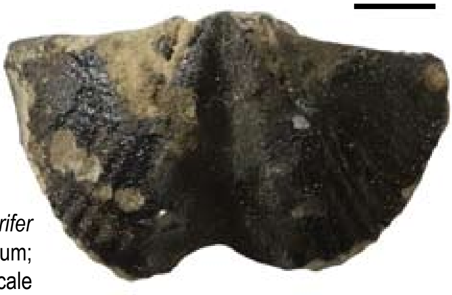

Fig. 18. Internal mold of the brachiopod *Orthospirifer milwaukeensis* (Cleland, 1911) covered with asphaltum; MPM 10978; Berthelet Member; collected by IE; scale bar 1cm.

Preservation of Color Patterns

Certain species from the Milwaukee Formation often preserve color patterns (Fig. 19). This mostly occurs with cranaenid and lingulid brachiopods, although it has also been observed with phacopid and proetid trilobites and the fin spines of certain fish, such as *Gamphacanthus*. These are typically seen as bands or spots with contrasting shades or hues. While there is little dispute that such patterns seen on brachiopod fossils are original surface features, there is some controversy regarding trilobites. It has been suggested that the color patterns of some trilobites may not have been visible from the surface of the living animal, and may instead show the placement of other structures, such as muscle attachments, slightly below the surface of the exoskeleton (Babcock, 1982). Other researchers interpret the spots and color bands of certain Devonian trilobites to be the original patterns that may have served as camouflage (McRoberts et al., 2013; Schoenemann et al., 2014). Due to the many chemical changes that take place during and after fossilization, in no cases are the actual colors of these patterns likely to be the same as when the animals were alive.

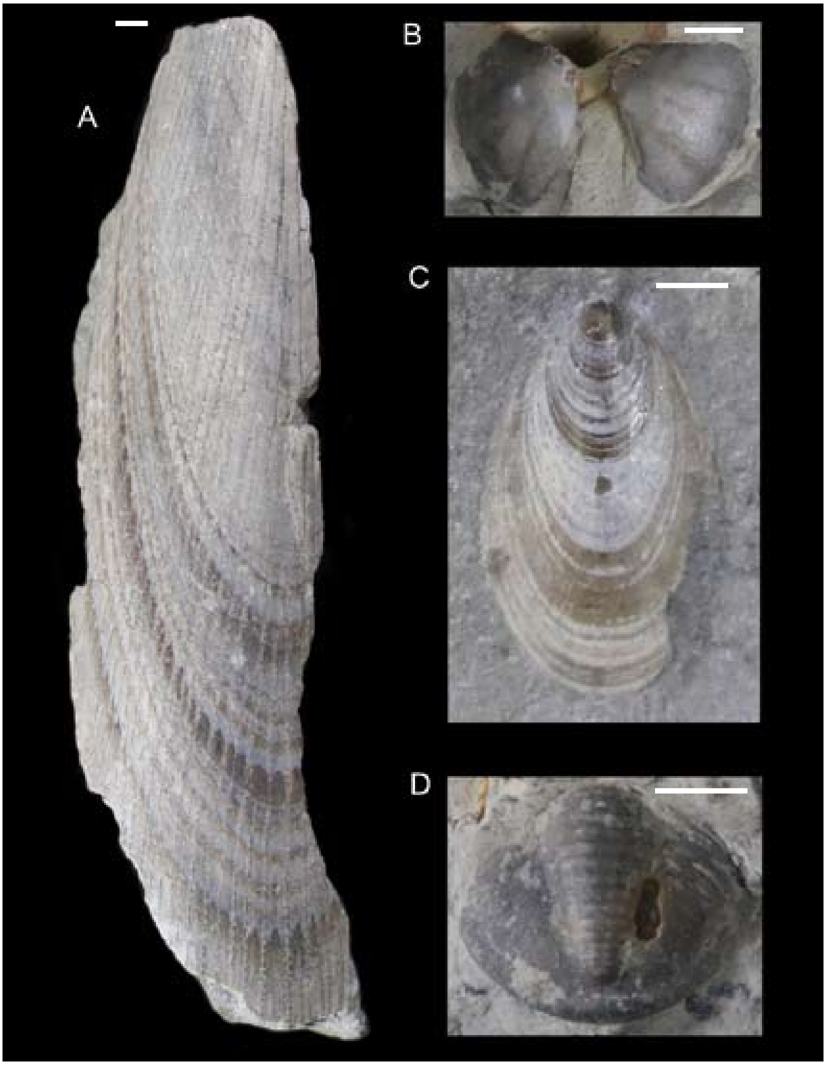

Fig. 19. Color patterns in skeletal materials. **A:** Fin spine from the ptyctodont *Gamphacanthus politus* (Newberry, 1889); UWM-GM 18269; Berthelet Member; scale bar 1cm. **B:** Splayed valves of the brachiopod *Cranaena* sp.; WESM-KCG 1115; Lindwurm Member; collected by LVS; scale bar 5mm. **C:** Brachial valve of the brachiopod *Barroisella? milwaukeensis* (Cleland, 1911); MPM 236; North Point Member; scale bar 1mm. **D:** Pygidium from a proetid trilobite; WESM-KCG 1049; Lindwurm Member; collected by JSG; scale bar 5mm.

Trace Fossils

Trace fossils are evidence of the movements or other behavior of an organism, as opposed to the organism itself. Most of the trace fossils of the Milwaukee Formation are in the form of burrows in the sediment. *Palaeophycus*, *Chondrites*, and *Zoophycos* are among its more common ichnogenera. These are discussed in more detail in Chapter 23.

Life and Death Assemblages

Throughout the Milwaukee Formation are layers that are packed with fossils on their surfaces (Figs. 20 & 21). These fossils are so prolific and well preserved that many observers enjoy imagining that they are viewing a snapshot of a seafloor with its natural assemblage of living creatures. Except for the color discrepancies we discussed above and the fact that all soft-bodied creatures have been removed from the

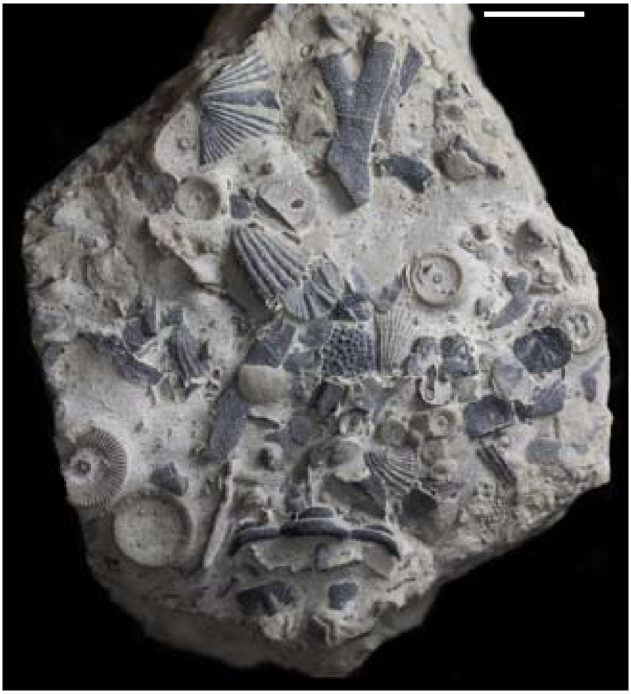

Fig. 20. Associated pieces of brachiopods, bryozoans, crinoid columnals, and trilobites. Such associations are typical of certain layers in the Lindwurm Member. MPM P26725; collected by LVS; scale bar 1cm.

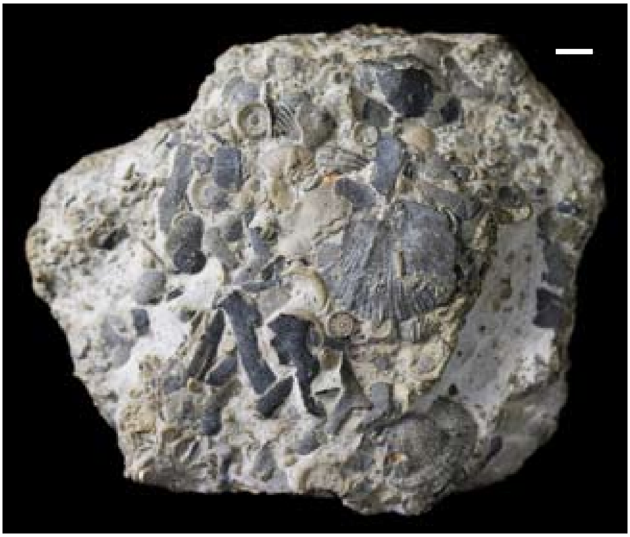

Fig. 21. Slab containing numerous fragments of the calcareous skeletal materials from brachiopods, bryozoans, hederelloids. crinozoans, corals, and trilobites. WESM-KCG 1111; Lindwurm Member; collected by KMG; scale bar 5mm.

scene, many of these examples of fossilized “mini-ecosystems” may actually appear fairly similar to the way they looked in life. However, we must remember that weeks, months or years may have transpired before they were buried. During that time currents made them subject to minor transportation, redistribution, sorting and reorientation. In addition, remains of different generations and in some cases slightly different communities could accumulate in a single bed of fossils; this process has been termed “time-averaging”.

Various remains in these assemblages may have been transported—the question being to what degree. We thus look for clues. For example, we know that *Aulopora, Petrocrania* and *Microconchus* that are still cemented to other shells or massive bryozoan colonies were obviously not transported away from their hosts. In addition, complete remains of delicate skeletons such as articulated crinoids and trilobites have almost certainly been buried rapidly with little to no transport. Other lines of evidence are not as conclusive. Shells that are severely broken and worn were probably transported more than ones that were fossilized intact; however, the gases within a nautiloid shell can enable it to float for miles without breakage or appreciable wear. The exact location where that cephalopod lived and died is, therefore, difficult to ascertain. The plants and fungi fossilized in the Milwaukee Formation certainly lived on land. The more delicate, well preserved ones probably did not live too far from where they were preserved, while others might have floated in with the currents from many miles away. As with cephalopod shells and planktonic organisms, it may not be possible to determine their exact place of origin or the distance they travelled.

Quality of Preservation

While some fossils of the Milwaukee Formation can be very well preserved, showing fine details, non-mineralized tissues, or color patterns, others can be so poorly preserved as to be unidentifiable. This is especially true of the bryozoans and corals. Most of the interiors of those fossils from the Milwaukee Formation have been obliterated by dissolution and/or dolomitization (Fig. 22), thus obscuring important diagnostic features and causing identification to rely only on external features (Cleland, 1911).

As with any other problem being studied in paleontology and other sciences, what we learn is only as good as the totality of the evidence accumulated. For that reason, we must consider all lines of evidence and study as many fossils as we can in order to best describe and explain these ancient organisms.

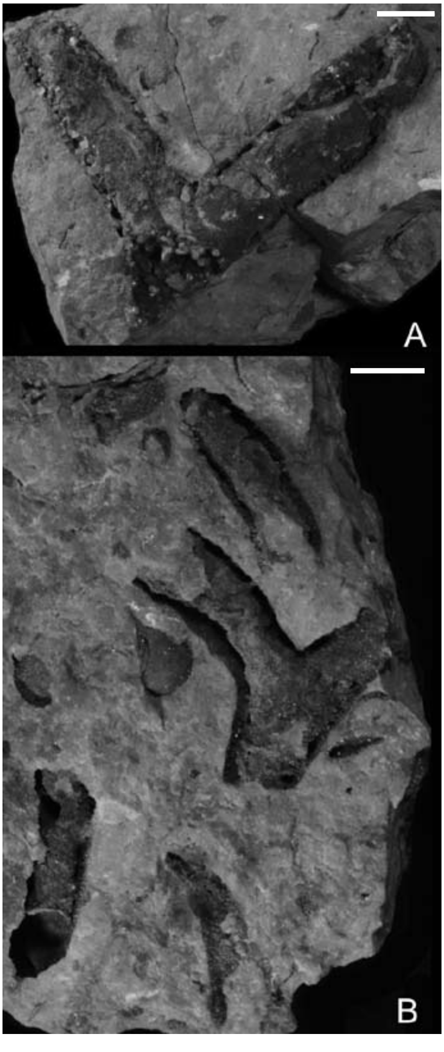

Fig. 22. Apparent ramose bryozoan zoaria; Berthelet Member; scale bars 1cm. Dissolution and recrystallization have obscured all internal and external identifying features. **A:** UWM-GM 9577; **B:** UWM-GM 9576.

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Glossary

Abaxial—Directed away from the longitudinal axis of an organism or structure.

Acanthodii—The class of teleosts having dermal and perichondral bone as well as a series of stout spines before its dorsal, anal and paired fins. This class was, for a short time, included within the Placodermi, but is now recognized to have more features in common with the Osteichthyes.

Actinoceratoidea—The subclass of cephalopods having shells of medium to large size ranging in shape from straight and slender to slightly curved, simple, curved septa and sutures, and typically a siphuncle that was broadly expanded between septa and at least partially filled with calcareous deposits.

Abaxial—Directed toward the longitudinal axis of an organism or structure.

Ambulacrum (pl. a)—Structure in echinoderms (generally five or multiples of five in number) in which food is conveyed to the mouth.

Ammonoidea—An extinct subclass of marine cephalopods bearing an external, chambered shell divided by partitions (septa) that have convoluted margins which are often sufficiently distinct to aid in identification of species.

Amphibian—Member of the Amphibia, a class of cold-blooded vertebrates having gilled aquatic larvae and air-breathing adults; includes frogs, toads, salamanders and newts.

Animalia (=Metazoa)—The kingdom of multicellular eukaryotes that typically feed on organic matter, process it in a central cavity, and are mobile for at least part of their lives.

Annelida—The protostome animal phylum of aquatic or terrestrial, vermiform, bilaterally symmetrical, coelomate metazoans that have a segmented external cuticle that is never molted; includes earthworms, leeches, marine worms and many other worn-like animals.

Anthozoa—A class of aquatic (mostly marine) polypoid cnidarians having a tubular body, tentacles around their mouths and generally sedentary adults. Unlike the other cnidarian classes, they do not have a medusa stage in their development. Includes corals, sea anemones, and sea fans.

Antrim Shale—An Upper Devonian formation lying unconformably on the Milwaukee Formation; known in Wisconsin only from glacial erratic blocks, float from tunnel excavations, and core samples; the Wisconsin material is the western-most occurrence of the Antrim Shale, which is found more extensively in Ohio, Indiana and the type locality, eastern Michigan.

Apatite—A group of calcium phosphate minerals whose members are major constituents of bones, teeth and certain shells and other skeletal materials of such invertebrates as lingulid brachiopods and the extinct conodonts and conulariids.

Aragonite—An unstable morph of calcium carbonate, generally having a pearly luster, found primarily in certain layers of the shells of brachiopods and mollusks; transforms into calcite over time.

Arborescent—Tree-like in form and size.

Archaebacteria (=Archaea)—The domain of single celled organisms that are essentially intermediate between the two other domains, Eubacteria and Eucaryota; includes forms that can live in extreme conditions such as hydrothermal vents, hot springs, and hypersaline water.

Argillaceous—Pertaining to rocks composed of grains less than 0.0625 mm in diameter, i.e., clay rich.

Arthropoda—The protostome animal phylum having a chitinous exoskeleton and typically segmented body with jointed legs; includes the chelicerates, trilobites, myriapods, crustaceans, insects, and many other living and extinct aquatic and terrestrial groups; the most diverse phylum of animals.

Articulated—Hinged or otherwise held together, generally via interlocking parts.

Asphaltum—A black, tar-like substance occurring in rock cavities and derived from life forms through natural processes.

Asterozoa—A more-or-less star-shaped class of echinoderms typically having five (or multiples of five) appendages, each with a series of tube feet (hydraulically operated by a water vascular system) on either side of the ambulacra; includes sea stars (starfish) and brittle stars.

Benthic—The marine zone including the region on or beneath the sea floor.

Berthelet Member—The lowest (oldest) member of the Milwaukee Formation, overlying the Thiensville Formation and underlying the Lindwurm Member; comprised of medium to thick bedded argillaceous limestone and argillaceous dolomite; fossils generally in the form of internal and external molds; the source of most of the Milwaukee Formation's fossil fish and land plants.

Biocalcarenite—A detrital carbonate rock composed of sand-sized particles largely derived from animal and/or protist shells.

Biota—The animals, plants, fungi and other life forms of a particular place, time, environment, or geological unit.

Bioturbation—The restructuring of sedimentary deposits by moving organisms.

Bivalvia—The class of aquatic mollusks that includes the clams, oysters, mussels and related forms typically possessing two calcareous shells that hinge together and enclose a muscular foot and other soft parts.

Blastoidea—An extinct class of echinoderms with biserial brachioles bordering their ambulacral areas, well developed pentameral symmetry, seventeen major plates (basals, radials and deltoids) arranged in three circlets, a lancet plate underlying its ambulacral system, an anus, mouth, hydrospires on either side of each ambulacrum crossing the plate suture, and typically a spiracle near the adoral extremity of each ambulacrum.

Blastopore—The first opening formed in the central cavity of an embryo during gastrulation.

Brachial valve (=dorsal valve)—Valve that invariably contains any skeletal support for lophophore and never wholly accommodates pedicle; commonly smaller than ventral valve and with distinctive muscle-scar pattern.

Brachidium (pl. a)—One of the pair of calcareous supports for the lophophore of brachiopods, in the form of a loop or spire.

Brachium (pl. a) (=arm)—In certain crinozoans (e.g., crinoids), one of the food-gathering appendages attached to the top of the calyx.

Brachiole—In blastoids, one of the slender food-gathering appendages attached to the lancet plates at the border of the ambulacra.

Brachiopoda—The lophophorate animal phylum consisting of solitary, marine, sessile, coelomate, metazoans having a pair of calcareous or chitinophosphatic valves that are bilaterally symmetrical about the median plane that is normal to the surface of separation between valves.

Breccia—Sedimentary rock composed primarily of large, angular or subangular fragments cemented by a matrix of smaller particles that may be of a different composition.

Bryozoa—The lophophorate animal phylum consisting of colonial, aquatic, generally sessile, polymorphic metazoans, regarded as coelomate, with a retractable food-gathering lophophore, U-shaped digestive tract and typically having a calcareous skeleton.

Calcareous—Composed largely or entirely of at least one morph of calcium carbonate.

Calcining—The heating of solids to a high temperature for the purpose of removing volatile substances, oxidizing a portion of mass, or rendering them friable.

Calcite—The most common morph of calcium carbonate; the primary mineral of which limestone and many calcareous shells are made.

Calyx (=Cup) (Zoological context)—The head region of a crinozoan exclusive of its brachia/brachioles, enclosing the main portion of the visceral mass.

Cambrian—The first period in the Paleozoic Era, ranging from about 541,000,000 to 485,000,000 years ago, from which the oldest abundant fossils are encountered; followed by the Ordovician Period.

Carboniferous—The period in the Paleozoic Era between the Devonian and Permian Periods, ranging from about 359,000,000 to 299,000,000 years ago.

Carina (pl. ae)—In conulariids, an internal, thickened ridge located along the corners and/or midlines of the periderm.

Caustic potash—Potassium hydroxide (KOH); a strong alkali once used to remove calcareous matrix from fossils; generally fallen into disuse due to its health hazards and destructive effects on the fossils themselves.

Cenozoic—The era following the Mesozoic Era, including the Paleogene, Neogene and Quaternary periods; last 65 million years of Earth history.

Cephalon (pl. a) (Zoological context)—The head region of certain arthropods, e.g., trilobites.

Cephalopoda—The class of agile, bilaterally symmetrical, predacious molluscan carnivores typically having a pair of complex eyes, a beak, a set of eight or more elongated, flexible appendages, and a funnel for propulsion through the water; have either a single calcareous external or internal shell or may lack a shell entirely.

Chaetognatha (=Arrow worm)—The phylum of planktonic and nektonic, coelomate, bilaterally symmetrical, mostly marine and predatory, wormlike animals.

Chert—An opaque sedimentary rock composed of extremely fine-grained crystals of silica.

Chimaeroidei—The chondrichthyan suborder that typically has grinding tooth plates and a prominent leading spine on the first dorsal fin; includes the ratfish.

Chitin (Biochemical context)—A stiffening yet flexible nitrogenous material of which fingernails, hooves and many invertebrate exoskeletons (especially arthropods) are primarily composed.

Chitinophosphatic—Composed of chitin and phosphates (especially calcium phosphate), such as the outer covering of conulariids and the shell of lingulid brachiopods.

Chitinozoan—Enigmatic, flask-shaped marine microorganisms or egg cases (Ordovician–Holocene) typically composed of chitin-like material.

Chondrichthyes—The class of gnathostomes having cartilagenous endoskeletons—the males having a pair of claspers; includes the sharks, rays, chimaeras, and related forms.

Chordata—The phylum of bilaterally symmetrical animals having a notochord and pharyngial gill slits in adults or certain embryological stages; includes the urochordates (tunicates), cephalochordates (lancelets), craniates, and, tentatively, conodonts.

Claspers—The paired organs of the male of certain animals, such as chondrichthyans and certain placoderms, used for stabilization during mating.

Class—The rank in taxonomic hierarchy between phylum and order.

Cnidaria—The phylum of acoelomate, headless, aquatic, predatory, colonial or solitary, polypoid or medusoid animals having a mouth surrounded by stinging-cell-bearing tentacles; includes corals, sea fans, hydroids, and jellyfish.

Coelacanthiformes—The sarcopterygian order that includes the extant *Latimeria*, classically labeled a "living fossil."

Coelom—A fluid-filled body cavity lined with mesodermal cells; found in vertebrates and many other bilaterally symmetrical animals.

Coleoidea—The subclass of cephalopods that includes most of the living forms, such as octopi, squids, and cuttlefish; typically shelless, but often with a hard internal structure, such as a gladius (in many squids), cuttlebone (in cuttlefish) or thickened rostrum (in the extinct belemnoids).

Column—In most stalked echinoderms, an elongated cylindrical structure on the aboral end of the calyx with which it attaches to the substrate at its other extremity; sometimes referred to as a stalk.

Columnal—The unit ossicle composing the crinozoan column; typically discoidal in shape.

Commensalism—A relationship between individuals of two species (A and B) in which A benefits from B without either harming or benefiting B.

Commensal—The species that benefits from the commensalistic relationship.

Conodonta—The class of small, marine, pelagic and benthic chordates of eel-like form having head regions containing assemblages of microscopic phosphatic tooth-like structures also termed conodonts.

Conulariida—The extinct group of sessile benthic, polypoid scyphozoan cnidarians having a steeply pyramidal, generally four-sided periderm constructed of alternating, extremely thin organic and apatitic lamellae that in some species could be folded to cover the oral end of the animal.

Corallite—The exoskeleton of a solitary polyp or of a bud in a colony of anthozoans.

Craniata—The chordate subphylum characterized by possession of a cranium.

Cranidium—In trilobites, the central portion of the exoskeleton of the cephalon bounded laterally by the facial suture.

Cretaceous—A period in the Mesozoic Era between the Jurassic and Tertiary, ranging from about 145,000,000 to 66,000,000 years ago.

Crinoid—Member of the Crinoidea, a class of stalked echinoderms with pentamerous symmetry and five (or multiples of five) outspread, branched, food-gathering arms (brachia).

Crinozoa—The subphylum of echinoderms typically attached by a stalk and possessing a calyx having ambulacra that served as food grooves extending outward onto projecting appendages (brachia or brachioles).

Crustacea—The subphylum of mandibulate arthropods typically having two pairs of pre-oral appendages; includes crabs, lobsters, isopods (wood lice), amphipods, copepods, ostracods and other living and extinct forms.

Ctenophora—The phylum of carnivorous, marine, generally free swimming animals placed until recently in the same phylum with the Cnidarians; unlike cnidarians, ctenophores lack stinging cells and bear few to no tentacles, having instead a series of ciliated combs for locomotion and a sticky substance for capturing prey; comb jellies.

Cyanobacteria (=Blue green "algae")—The phylum of photosynthetic eubacteria accounting for much Earth's oxygen; some types can form multicellular colonies of biofilms, biomats or stromatolites, in some cases working in symbiosis or metabolic cooperation with algae and other types of organisms.

Dendroidea—The order of sessile graptolites attached by the apex of the sicula, which is then generally more or less embedded in secondary cortical tissue forming a root-like base.

Dermal plate—One of the bony plates hinged or joined together in the head and thoracic regions of placoderm fishes forming a body armor either on the surface or beneath a layer of skin.

Deuterostomia—The subkingdom of animals having a mouth that delelops from a secondary opening in the embryonic gut other than the blastopore; includes the Bryozoa, Brachiopods, Chaetognatha, Echinodermata, Hemichordata, and Chordata, and several minor phyla.

Detritus—Loose material, such as rock fragments or organic particles, that results directly from disintegration rather than from crystallization or other means.

Detrivore—One who feeds on detritus.

Devonian—The period in the Paleozoic Era between the Silurian and Carboniferous Periods, ranging from about 419,000,000 to 359,000,000 years ago; the period in which the Milwaukee Formation was deposited.

Disarticulated—Unhinged or otherwise disjoined.

Disconformity—An unconformity such that the beds above and below the surface are parallel.

Dissolution (Geological context)—The breakdown of a material into individual ions, atoms or molecules by water or other solvents.

Dolomite—The mineral calcium magnesium carbonate, generally including lesser amounts of iron in place of the calcium and magnesium.

Dolomitization—The process by which limestone (calcium carbonate) transforms to dolomite via replacement of some of the calcium ions by magnesium ions.

Domain—Generally regarded as the highest rank in taxonomic hierarchy, positioned immediately above kingdom.

Dorsal valve (=brachial valve)—Valve that invariably contains any skeletal support for lophophore and never wholly accommodates pedicle; commonly smaller than ventral valve and with distinctive muscle-scar pattern.

Doublure—In trilobites, the reflexed continuation of the dorsal exoskeleton onto the ventral surface.

Dysaerobic—Pertaining to a depositional environment having 0.1 to 1.0 ml of dissolved oxygen per liter of water.

Echinodermata—The deuterostome animal phylum of coelomate, marine, benthic (exceptionally pelagic) metazoans lacking a differentiated head or brain and typically having pentamerous symmetry, an endoskeleton formed of plates and other distinct ossicles composed of crystalline calcite, and a water vascular system; includes the familiar starfish and brittle stars (Asterozoa), sea urchins, sand dollars, and sea cucumbers (Echinozoa), sea lilies and related forms (Crinozoa), and lesser known living and extinct subphyla.

Echinozoa—The subphylum of echinoderms with radial symmetry, meridional pattern of growth producing an essentially globoid body, but no projecting appendages.

Ediacaran—The last period of the Neoproterozoic Era, ranging from about 635,000,000 to 543,000,000 years ago, followed by the Cambrian Period.

Edrioasteroidea—The class of sedentary, stalkless, radiate echinozoans that had a domal, clavate, or globose polyplated theca; ambulacra (generally five) endothecal, formed by floor plates and cover plates.

Embryophyta—The group of photosynthetic plants distinguished from the other plants by producing embryos that it nurtures within its body; includes mosses and all other land plants.

Endochondral bone—Cellular bone that develops by replacing cartilage with bone; typically found in the long bones of the skeleton.

Endoskeleton—A skeleton located within the body of certain organisms such as vertebrates, echinoderms, and various mollusks, for the purpose of muscle attachment, protection of internal organs, or both.

Epibiont—An organism that lives on and generally attaches to another organism.

Epifauna—Benthic fauna living on the substrate or on other organisms.

Eubacteria—Procaryotic organisms having a simple RNA structure and specific cell wall chemistry.

Eucaryota—The domain of organisms that contains cell nuclei and organelles; includes all organisms except eubacteria and archaeobacteria.

Euthycarcinoid—The enigmatic, mandibulate arthropod having a segmented tail region and up to twenty-eight pairs of undifferentiated walking legs; Middle Cambrian to Triassic.

Evaporitic—Pertaining to deposits of minerals precipitated when evaporation in a body of water exceeds the rate of introduction of additional water.

Exoskeleton—A stiffened external protective and supportive covering on certain animals, especially invertebrates.

External mold—Sediment that surrounds the outside surface of a shell or skeleton, that shows an impresson of the outside of the shell or skeleton, often showing external shell structures such as growth lines and ornamentation.

Facial suture—In trilobites, the suture bounding the adaxial margin of the eye surface; has anterior and posterior branches, each of which may extend over the border and onto the doublure; separates free cheek from fixed cheek.

Family—The rank in taxonomic hierarchy between order and genus.

Fenestrate—In bryozoans, a growth habit modification in which slender branches separated by rectangular open spaces called fenestrules are arranged in a reticulate pattern to form broad fronds.

Fixed cheek (=Fixigena)—In trilobites, the portion of the cranidium abaxial to the axial and preglabellar furrows and imaginary sagittal line bisecting the frontal area.

Foraminiferida—The phylum of amoeboid, unicellular protists that are generally microscopic, marine and include a chambered shell with foramen (perforations).

Free cheek (=Librigena)—In trilobites, the portion of the cephalon abaxial to the facial suture.

Fucoid—A member of or resembling the algae *Fucus*.

Fungus—The kingdom of single or multi-celled eucaryotes that typically have a system of filliments and spores; includes such organisms as mushrooms, yeasts, and molds; considered more similar to animals than to plants.

Funnel—See hyponome.

Gastropoda—A diverse class of vagile aquatic or terrestrial mollusks, including snails and slugs, that typically have a spiral calcareous shell, although some shells are conical, cap-shaped or absent.

Genus—The rank in taxonomic hierarchy between family and species.

Geode—A cavity in a rock or fossil that has become lined with one or more layers of a mineral, generally silica or calcite.

Glabella—The central portion of the cranidium of a trilobite.

Gnathostomata—The superclass of craniates that have jaws; the jaws are derived from modified gill arches; this group includes the classes Placodermi, Chondrichthyes, and the grade Teleostomi, which in turn includes the classes Acanthodii and Osteichthyes.

Graptolithina—The class of sessile or pelagic colonial marine hemichordates that secreted a sclerotized exoskeleton with characteristic growth bands and growth lines; the thecae housing individual zooids were usually arranged in a single or double row along the branches (stipes) of the colony (rhabdosome); rhabdosomes originated by a single bud from the initial zooid, housed in a conical sicula, producing simple, branched or rarely encrusting colonies.

Hemichordata—The deuterostome animal phylum generally having embryonic pharyngeal openings but lacking the endostyle and notochord distinctive of the chordates.

Hold-fast—The root-like or disc-shaped structure at the distal end of a crinozoan's column used to anchor the animal to the substrate.

Holocene—The current epoch; in the Quaternary Period, following the Pleistocene Epoch, ranging from about 11,700 years ago to the present.

Hydraulic cement—Cement that chemically reacts and hardens with water, and is capable of doing so under water.

Hydrospires—Thin-walled, folded structures within the calyx of blastoids believed to have aided in respiration.

Hydrozoa—The class of generally carnivorous, colonial cnidarians having a tubular body, a vellum that aids in swimming in medusae, tentacles around their mouths that lack stinging cells, and may have either a polypoid stage, medusa stage, or both. The skeletons of colonial forms are generally chitinous, but calcareous in some species.

Hyolithida—The extinct group of probable lophophorates whose calcareous fossils include bilaterally symmetrical, conoidal sclerites that are open at their wider ends, an operculum, and a pair of lateral spines.

Hyponome (=Funnel)—In cephalopods, the fleshy tube used to propel the animal by forcing water through it.

Hyponomic sinus—In nautiloid and ammonoid cephalopods, the indentation of the shell's aperture through which the hyponome extends outside of the living chamber.

Hypostome—In trilobites, a plate attached to the ventral side of the carapace beneath the glabella; believed to have been related to feeding.

Ichnogenus—A group of related ichnospecies.

Ichnospecies—The lowest rank in the hierarchy of trace fossil taxa.

Infaunal—Living within the sediment beneath a body of water.

Infraphylum—The rank in taxonomic hierarchy between subphylum and class.

Internal mold—Sediment filling the inside surface of a shell, often showing impressions of internal shell structures such as muscle scars.

Jurassic—The period in the Mesozoic Era between the Triassic and Cretaceous Periods, ranging from about 201,000,000 to 145,000,000 years ago.

Lake Church Formation—The Middle Devonian formation in southeastern Wisconsin that immediately underlies the Thiensville Formation and, depending on the exact location, overlies either the Waubakee Dolomite or Racine Dolomite.

Lancet plate—Elongate spear-shaped plate inserted between the deltoids of blastoids. The brachioles are attached to these plates.

Lindwurm Member—The member of the Milwaukee Formation between the Berthelet and North Point Members; more thinly bedded and fossiliferous than the Berthelet Member.

Linguliformea—The subphylum of brachiopods having organophosphatic stratiform shells that are not articulated or with rudimentary articulation not involving teeth and sockets, and possessing a pedicle formed as an extension of the ventral body wall.

Lophophorate—A group of lophophore-bearing coelomate organisms that includes brachiopods, bryozoans, and phoronids.

Lophophore—A ciliated structure used by certain aquatic animals, such as brachiopods, bryozoans, phoronids, and hyoliths, to gather and transport food to the mouth.

Lycophytina—Tracheophytes having leaves arranged in a dense, regular spiral pattern that result in distinctive scar patterns in the deciduous members of the group; leaves are narrow and typically with one unbranched vein; some Middle Devonian through Carboniferous forms were arborescent; lycopods.

Keratinous—Composed of the fibrous protein, keratin; the main constituent of hair, feathers, nails, hooves, and horns.

Kingdom—The rank in taxonomic hierarchy between domain and phylum.

Lycopod (=lycophyte)—A member of the Lycophytina

Malacostraca—The class of crustaceans with a carapace of widely varied form typically covering all or most of the head and trunk regions; head typically bearing paired compound eyes commonly located at tips of movable eye stalks, with five pairs of appendages behind the eyes (antennules, antennae, mandibles, maxillules and maxillae); trunk composed of eight thoracic somites and six or seven abdominal somites, most equipped with paired appendages; includes crabs, lobsters, and crayfish.

Mandible—The chitinous chewing structure found in millipedes, crustaceans, insects and certain other living and extinct arthropods; also the lower jaw of vertebrates.

Marcasite—The morph of the mineral iron sulfide (FeS_2) in the orthorhombic crystal system and is tin white in color on freshly fractured surfaces, but quickly weathers to ferrous sulfide, which is crumbly and orange in color.

Medusoid—Having the mode of life, form, orientation of a medusa, thus being free-swimming, having an umbrella-shaped body, with a mouth and tentacles facing ventrally.

Membrane bone—Bone that forms in membranous tissues and not as a replacement of cartilage.

Meridional—Pertaining to a meridian, which is a line running from pole to pole of a rounded structure; describes the pattern of growth found in echinoids and holothurians (sea cucumbers).

Mesenteries—In anthozoans, the vertically-oriented sheet-like partitions that radiate inward from the body wall toward the central cavity of the polyp; the organs of digestion, adsorption and excretion, and the site of development of the gonads.

Mesozoic—The era immediately following the Paleozoic and preceding the Cenozoic Eras, beginning with the Triassic Period and continuing to the Cretaceous Period.

Metazoa—See Animalia.

Microconchida—The order of encrusting tentaculitoids having a small, spiral shell.

Millerite—The mineral nickel sulfide (NiS); metallic pale brass-yellow crystals frequently forming as radiating needles associated with calcite; sometimes secondarily altered on its surface to emerald green zaratite (hydrous nickel carbonate).

Millipede—A member of the myriapod class Diplopoda, which is typically characterized by possession of an elongated, cylindrical body and numerous pairs of legs distributed as two pairs per segment.

Milwaukee Cement Company—A large producer of hydraulic cement located at the northeast side of Milwaukee, Wisconsin, and operating between 1876 and 1909. The source rock was certain layers (primarily the Berthelet Member) of the Milwaukee Formation.

Milwaukee Formation—A Middle Devonian (Givetian) formation located in Milwaukee County, Wisconsin, and lying above the Middle Devonian Thiensville Formation and below the Upper Devonian Antrim Shale; contains a diverse biota of fossilized invertebrates, fish, and rare land plants; consists of three members, in ascending order: Berthelet, Lindwurm and North Point.

Mollusca—The protostome animal phylum consisting of aqueous and terrestrial, nonsegmented (except for the Polyplacophora) invertebrates having a fleshy mantle that secretes a calcareous shell of one or more pieces. The shell may be exteriorly-facing, enclosed by the mantle, reduced or lost; includes snails, clams, squids and related forms.

Monophyletic—A relationship among a group of organisms in which the group is descended from a common ancestor, and includes all of the descendant groups.

Monticule—In some bryozoans, a cluster of polymorphs which makes a prominence on the surface of the zoarium; a macula.

Natural reef—A large subaqueous moundlike structure composed of the skeletons of various organisms such as corals, bryozoans and/or other biota that secrete calcareous skeletal materials; typically includes the living producers of these materials and a diverse and prolific community of other species that also inhabit the reef. Although the Milwaukee formation contained bryozoans and corals, it lacked reef structure.

Nautiloidea—The subclass of cephalopods having small to large external shells ranging in shape from straight to tightly coiled, simple, curved septa and sutures, and lacking the close-packed endocones or complex annular deposits characteristic of some of the other subclasses.

Nekton—Animals that swim freely against currents.

Neogene—The period in the Cenozoic Era between the Paleogene and Quaternary Periods, ranging from about 23,000,000 to 2,600,000 years ago.

Neoproterozoic—The era preceding the Paleozoic Era.

Nitrogenous (Biological context)—Containing nitrogen, such as chitin, skin and many other biologically produced materials.

North Point Member—The youngest member of the Milwaukee Formation, lying above the Lindwurm Member and below the Upper Devonian Antrim Shale; lithologically similar to and apparently continuous with the Lindwurm Member, but contains many silicified fossils.

Notochord—One of the defining features of the Chordata, consisting of a rod-like flexible embryonic structure that persists in the adults of certain subphyla and contributes to the ossification of vertebrae in the vertebrates.

Operculum—The keratinaceous or calcareous plate attached to the foot of many gastropods for partial or complete closure of the aperture.

Order—The rank in taxonomic hierarchy between class and family.

Ordovician—The period in the Paleozoic Era between the Cambrian and Silurian Periods, ranging from about 485,000,000 to 444,000,000 years ago.

Ossicles—The discrete calcareous entities that comprise the exoskeleton of echinoderms or are embedded in their skin, providing support, protection and defense.

Osteichthyes—The class of gnathostomes having endochondral or membrane bone; skull with sutures; lung(s) usually present, functioning either as air-breathing organs or as buoyancy-controlling swimbladders or both; includes the Sarcopterygii and the Actinopterygii.

Ostracoda—The class of crustaceans that is aquatic, semi-microscopic, kidney bean-shaped, bi-valved, and mostly free-swimming.

Otoliths—Calcareous bodies within the inner ear of teleosts; play a critical role in the sense of balance.

Paleogene—The first period in the Cenozoic Era, between the Cretaceous and Neogene Periods, ranging from about 66,000,000 to 23,000,000 years ago.

Paleozoic—The era between the Neoproterozoic and Mesozoic Eras, beginning with the Cambrian Period and ending with the Permian Period.

Paraphyletic—A relationship among a group of organisms in which the group is descended from a common ancestor, but does not include all of the descendant groups; e.g., Pisces, which was defined to exclude the Tetrapoda, which is believed to have descended from the same common ancestor.

Pedicle—The fleshy organ of a brachiopod with which the animal typically attaches to the substrate.

Pedicle valve (=ventral valve)—Valve through which pedicle commonly emerges, usually larger than dorsal valve and invariably containing teeth when present.

Pedogenic—Pertaining to the formation and development of soils and related sediments.

Pelagic—The marine zone that includes the entire column of water above the benthic zone.

Perichondral bone—Bone that is typically thinly laminated, acellular, surrounds the soft tissues and is ossified from a layer of tissue that surrounds the cartilage as it develops.

Periderm—The thin, flexible organo-apatitic covering of a conulariid.

Permian—The last period in the Paleozoic Era, between the Carboniferous and Triassic Periods, ranging from about 300,000,000 to 250,000,000 years ago.

Permineralization—The fossilization process in which calcite or to a lesser extent silica or other dissolved minerals in the groundwater crystallize within the pores of skeletal remains.

Phanerozoic—The eon following the Precambrian, ranging from about 541,000,000 years ago to the present.

Phoronida—The phylum of solitary lophophorate metazoans having a long, flexible tube-like body.

Phyllocarida—The order of malacostracan crustaceans whose head and thoracic regions are encased in a bivalved chitinous carapace.

Phylum (pl. a)—The taxonomic rank typically lying between the rank of kingdom and class or subphylum.

Pinnules—Fine projections of certain crinoid arms that may be used as filters during feeding.

Pisces—The name of a subdivision of vertebrates previously used to include what were considered to be fishes and to exclude tetrapods; generally abandoned due to the paraphyletic nature of the group.

Placodermi—The class of marine and freshwater gnathostome (jawed) craniates having a mostly cartilaginous endoskeleton and boney dermal plates covering their head and trunk.

Plankton—Animals and plants that float or drift in a body of water, but are unable to swim against the currents.

Polychaeta—The diverse class of mostly marine annelids that typically bear unjointed appendages that develop as extensions of the animal's body segments.

Polypoid—Having the mode of life, form, orientation of a polyp, thus typically being attached at its base, with a mouth and tentacles facing dorsally.

Pleistocene—The first epoch of the Quaternary Period, between the Pliocene and Holocene Epochs, ranging from 2,580,000 to 11,700 years ago.

Polymorphic (Biological context)—Having more than one form within the same species, each generally having its own function; e.g., honey bees with their drone, worker, and queen morphs.

Precambrian—The eon prior to the Phanerozoic, beginning with the formation of Earth (about 4,600,000,000 years ago) and ending about 541,000,000 years ago.

Prokaryota—The domain of single-celled organisms that lack a nucleus and organelles.

Protista—The kingdom of eukaryotic organisms that are typically microscopic and single-celled or in the form of colonies of identical cells.

Protostomia—The subkingdom of animals having a mouth that delelops from the first opening into the embryonic gut (blastopore); includes the Mollusca, Annelida and Arthropoda.

Ptyctodontiformes—The placoderm order characterized by its sturdy, blunt, frequently textured chewing surfaces presumably specialized for crushing shells.

Pygidium (pl. a)—In trilobites, the posterior portion of the exoskeleton separated from the thorax by articulation.

Pyrite—The morph of the mineral iron sulfide (FeS_2) that is in the cubic crystal system and metallic brassy yellow in color; weathers to limonite; "fools' gold."

Quaternary—The current geological period, following the Neogene Period, ranging from 2,580,000 years ago to the present.

Radiolaria—The phylum of protists bearing a siliceous test of varying shapes and intricate designs.

Radula—The keratinaceous, tongue-like structure in the mouth of most mollusks used for rasping food off a surface or drilling into shells.

Ramose—Branching, as in ramose corals or bryozoans.

Replacement (Paleontological context)—A type of fossil preservation in which groundwater-derived minerals entirely replace the skeletal materials of the organism.

Reptant—A growth habit of such colonial animals as certain corals and bryozoans, in which the colony is typically chainlike, branching and attached to the substrate by most or all of its habitation cells.

Rhabdosome—The sclerotized exoskeleton of an entire graptolite colony.

Rheophilic—Preferring or living in flowing water.

Rhombohedral cleavage—The tendency of minerals in the hexagonal crystal system to break in pieces having the shape of a rhombohedron.

Rugosa—The extinct order of anthozoan cnidarian corals that were sessile, marine, calcareous, generally cone-shaped, solitary, and distinguished from each other largely by features relating to their septa.

Sabkha—A coastal region subject to extensive flooding and evaporation, typically resulting in the deposition of salts; a salt flat.

Sarcopterygia—The subclass of Osteichthyes consisting of lobe-finned fish and tetrapods.

Schizochroal—Pertaining to a type of trilobite eye in which its visual surface consists of a number of biconvex lenses, rounded or polygonal in outline, each lens covered by an individual cornea and separated from others by sclerotic walls.

Schott—In conulariids, a transverse wall in the apical region of the periderm; may have been a repair structure produced in response to mechanical severance of the body.

Sclerite—A sclerotized structure or section of one that adds rigidity and may serve other functions in various animals, especially arthropods; examples include a cephalopod's beak and a lobster's exoskeleton, which is composed of many sclerites.

Sclerotized—Hardening of the cuticle of an organism, such as an arthropod's outer covering or the human fingernail, whereby a more rigid organic substance, especially sclerotin, is produced.

Scolecodont—The chitinous jaw of a polychaete worm.

Scyphozoa—The class of the Cnidaria whose members are marine and, unlike medusoid Hydrozoa, have stinging cells on their tentacles, lack a vellum, and typically have a four-partitioned body and medusoid adults.

Sea pen—A member of the anthozoan order Pennatulacea, named for their resemblance to quill pens.

Segment—The exoskeleton of a somite, generally of the thoracic region of an arthropod.

Septum (pl. a)—A calcareous partition between the chambers of certain cephalopod shells, such as nautiloids, the extinct ammonoids, and other cephalopods that bear an exterior shell. Also, in certain anthozoans such as rugose corals, a radially disposed longitudinal partition of a corallite.

Sessile—Attached to the substrate, incapable of self-propulsion.

Sicula—The skeleton of the initial zooid of a colony of graptolites.

Silica—The colorless mineral SiO_2, belonging to the hexagonal crystal system and one of the most abundant minerals in Earth's crust; includes the familiar quartz, chert, and other lesser known morphs.

Siliceous—Composed of or containing silica.

Silicified—A type of fossil preservation in which the skeletal remains are replaced by silica.

Silurian—The period in the Paleozoic Era between the Ordovician and Devonian Periods, ranging from about 445,000,000 to 419,000,000 years ago.

Siphuncle—In externally-shelled cephalopods, the long slender or thick tube extending through all chambers to the apex and consisting of soft and shelly parts.

Somite—A transverse division of the body of an arthropod.

Species—Generally the lowest rank in taxonomic hierarchy, below genus; may be subdivided into subspecies or varieties. Members of the same species are normally capable of breeding and producing fertile offspring, in contrast to members of different species.

Sphalerite—The mineral zinc sulfide (ZnS), in the cubic crystal system, and often of a brown to black, though variable, color; frequently found in octahedral form and associated with other sulfide minerals and calcite.

Spionida—An order of tentacle-bearing polychaete worms.

Spiracles—Small openings on the summit of the calyx of blastoids through which it is believed water was passed for respiration.

Spire—In gastropods, the volutions of the shell past the first volution, generally described in terms of its relative height, with spire height generally increasing with successive volutions.

Sporangia—Structures within which spores are produced.

Stalk—An elongated structure between an eye and the rest of the body, as in malacostracans, or between the rest of the organism and the substrate to which it is attached, as in conulariids and crinozoans. See Column.

Stipe—In graptolites, one branch of a branched rhabdosome or the entire colony of an unbranched rhabdosome.

Stratigraphy—The study of the successions of layered rocks, what they reveal concerning changes that have taken place at that region, their use in correlating with successions in other regions, and helping locate mineral deposits of economic interest.

Stromatolites—Laminated dome-like, sheet-like or branching structures comprised of finely laminated calcareous layers formed by cyanobacteria, contributing to free oxygen production and reef-building since Precambrian time.

Stromatoporoidea—An enigmatic extinct group of colonial, calcareous major reef-builders in the Paleozoic Era consisting of laminae and pillars; may have been poriferans (sponges).

Suspension-feeder—An organism that feeds on materials that are suspended in the water.

Suture—In externally-shelled cephalopods, the line of junction of the free part of the septum and inner side of the shell wall.

Symbiosis—A relationship between individuals of two species of oganisms in which at least one species benefits; the relationship may benefit, harm or have no effect on the other species.

Tabula (pl. ae)—In rugose and tabulate corals, transverse partition of the corallite, extending to the outer wall or inner marginal wall.

Tabulata—The extinct order of almost exclusively Paleozoic, marine, calcareous, colonial, anthozoan cnidarians characterized by their exoskeleton of slender tubes crossed by many tabulae.

Taxon (pl. a)—Any unit used in the formal classification of organisms; e.g., kingdom, order, species, division, etc.

Tegmen—In crinoids, the adoral part of the theca above the origin of free arms or occupying the space between them; may be calcified or not.

Teleostomi—The grade of gnathostomes that includes the classes Acanthodii and Osteichthyes; have three pairs of otoliths.

Tentaculitida—The order of the Tentaculitoidea that had shells that were typically small (1–80mm), conical in shape, had transverse rings and, in some species, transverse and/or longitudinal striations—the transverse ones being growth lines.

Tentaculitoidea—An extinct group of enigmatic, generally marine animals that bore a conical or spiral calcareous shell and included the suborders Tentaculitida, Microconchida, and Cornulitida.

Terrestrial—Living exclusively on land.

Theca (pl. ae)—In graptolites, the sclerotized tube or cup enclosing any zooid of the rhabdosome other than the sicula. In crinozoans and echinozoans, the cup-shaped or globoid plated test of the animal enclosing the main part of the visceral mass; the cup (calyx) of a crinozoan, especially of a blastoid.

Thiensville Formation—The Middle Devonian formation that underlies the Milwaukee Formation.

Trace fossil—The fossilized markings or structures made by the activity of an organism on or within a substrate or another organism; the fossilized evidence of the locomotion, movements, industry, or other behavior of an organism, as opposed to the organism itself; includes, tracks, trackways, burrows, borings, resting traces, nests, feces, etc.

Tracheophytes—Vascular plants.

Triassic—The first period in the Mesozoic Era, ranging from about 250,000,000 to 200,000,000 years ago; followed by the Jurassic Period.

Trilobita—The common and extremely diverse subphylum of marine Paleozoic arthropods characterized by a calcite-impregnated exoskeleton divided longitudinally into three lobes.

Turbid—A condition of water in which particles are suspended, thus lowering clarity and light transmission.

Unconformity—A plane of contact between two successions of strata, representing a hiatus in the geologic record due to erosion and/or non-deposition of sediment.

Vagile—Free to move about.

Ventral valve (=pedicle valve)—Valve through which pedicle commonly emerges, usually larger than dorsal valve and invariably containing teeth when present.

Vermiform—Having the form of a worm.

Vug—A cavity in a rock typically formed by disintegration or dissolution of an embedded organism or other structure, and often partially or completely filled with a mineral of a different composition than the surrounding rock.

Water vascular system—In echinoderms, a hydraulic mechanism consisting of an assemblage of canals and associated specialized structures used to assist in feeding, locomotion, respiration and other important functions.

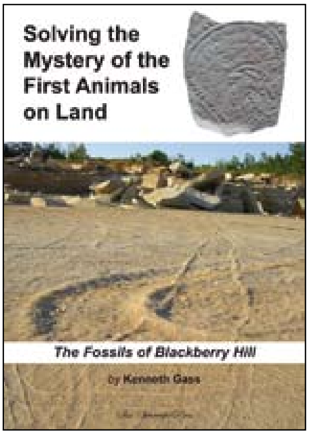
Whorl—One 360-degree rotation of a spiral shell such as that of many gastropods.

Zooecium—The skeleton of a bryozoan zooid, consisting of calcareous layers of zooidal walls and any connected intrazooidal calcareous structures.

Zooid—In graptolites, the soft-bodied individual inhabiting the theca. In bryozoans, one of the physically connected, asexually replicated morphologic units which, together with multizooidal parts and any extrazooidal parts present, compose a colony.

Zoarium (pl. a)—A colony of bryozoans.

Also by Kenneth C. Gass


Solving the Mystery of the First Animals on Land
The Fossils of Blackberry Hill
by Kenneth Gass

Siri Scientific Press (2015) 978-0-9929979-5-3 RRP £17.50
96 pp, 210 x 148 mm, soft cover,
81 colour illustrations, mainly photographs
Available at: www.siriscientificpress.co.uk

Reviews

Newsletter of the Paleontological Society (Priscum, Fall 2017, pages 19–20): "The photographs of the traces are extraordinary in their definition and clarity, and bring to life most vividly the activities of the animals. These trace fossils are of the greatest importance, as they are direct evidence that the beginnings of animal life leaving the sea for life on land began during the 540-500 million years of the Cambrian period, and not many millions of years later during the Silurian and Devonian periods."

Newsletter of the Palaeontological Association (2016, number 91, pages 107–108): "To cite the author from his first line of the preface to the book: 'A picture book on Blackberry Hills was inevitable. The place is simply too intriguing to remain buried in scientific journals…' I couldn't agree more." ... "... an excellent introduction for readers who want to dig deeper into the topic and the technical literature. Based on this I would recommend this book to all with an interest in natural history, scholars as well as amateurs."

Fossil News (Fall 2016: 51, abridged snippets): "...a beautiful, extensively illustrated book on one of the more important Middle Cambrian trace fossil deposits in the United States (the book contains 81 high-quality figures, most of them in colour and published only in this volume). …a great addition to the library of anyone interested in trace fossils, Cambrian life, or the early invasion of land. For professionals, the book offers excellent images of the trace and body fossils of Blackberry Hill, as well as an extensive reference list. For amateur paleontologists, it provides a nice introduction to the importance of trace fossils in the fossil record (and includes a thorough terminology section, which helps with understanding the geological, ichnological and biological terms used throughout the text).

Niles Eldredge, evolutionary biologist: "A mystery revealed, this book charmingly tells the story of how clever scientific detective work has answered the question of what those first animals to visit the subaerial environments of our world really were – however fleeting their visits from their ancient ocean habitats may have been. Engagingly told by Chris Gass, one of the key participants, the story reveals the importance of a highly special area that holds the fossilized evidence that shows what really happened."

Gregory D. Edgecombe, The Natural History Museum (London): "The early history of life on land is a conundrum that has perplexed some of the foremost figures in the history of paleontology since the era of Richard Owen and Charles Darwin over 150 years ago. At centre stage in this mystery are trackways on sedimentary rocks that we now know are of Cambrian age - some 500 million years old - and were made by animals making the first excursions out of water in life's history. Here, Chris Gass weaves together the history of science and groundbreaking research conducted over the past 20 years to reveal the identities of these ancient trace makers. His book is a scientific detective story in words and photographs."

From the back cover

Solving the Mystery of the First Animals on Land: The Fossils of Blackberry Hill is the first book to cover the unique group of rock outcrops in central Wisconsin that appears to have put an end to a 150 year-old mystery of global interest. Since the mid-1800s, fossilized trackways and footprints have been found on beach deposits that date back to the Cambrian Period, some 500 million years ago in what is now North America – but fossils of the animals that made them were reluctant to reveal themselves. Thanks to Blackberry Hill, the identity of some of the first animals to walk on land is a secret no more.

Numerous color photographs of spectacularly preserved tidal flat trackways, animals, and parts of the habitat itself, all set in stone, help to tell the story of some of the first animals to explore this strange, new, and presumably hostile environment. Current interpretations made possible by the fossil discoveries are presented, including how some of the trackways were made and what might have lured the animals ashore. Peculiar, winding trackways from giant, slug-like organisms and other boneless animals are shown covering entire surfaces. This book also reveals other surprises discovered at Blackberry Hill, including body and trace fossils of another tidal flat dweller never before found in rocks as old as these, and the first evidence showing that large jellyfish were abundant in Cambrian times and were already subject to mass strandings. In this book, Kenneth (Chris) Gass thus demonstrates why Blackberry Hill holds a special place in the history of life on Earth.

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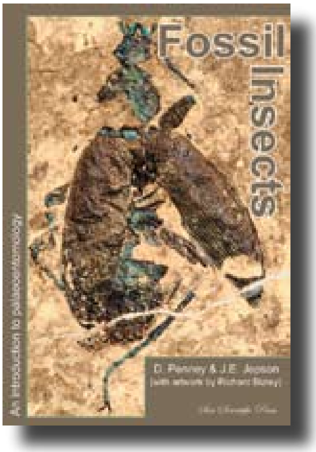

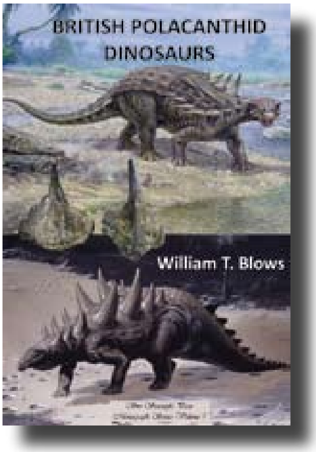

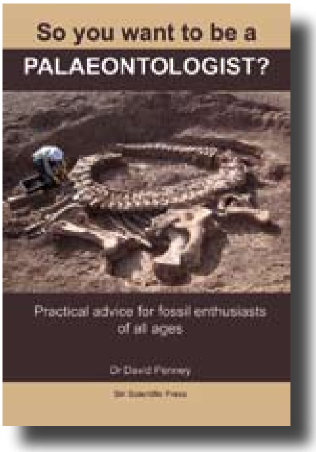

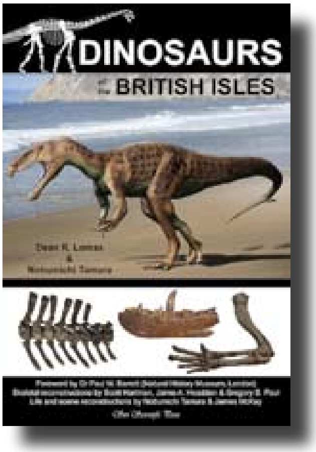

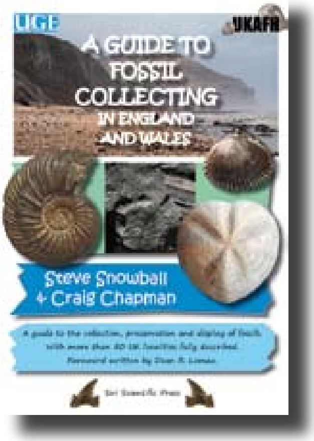
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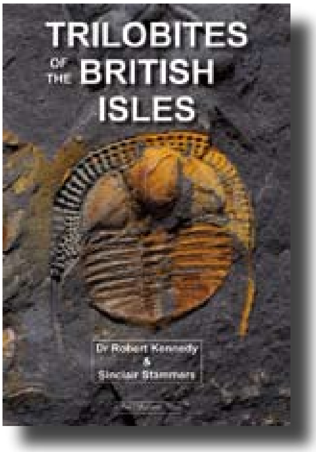

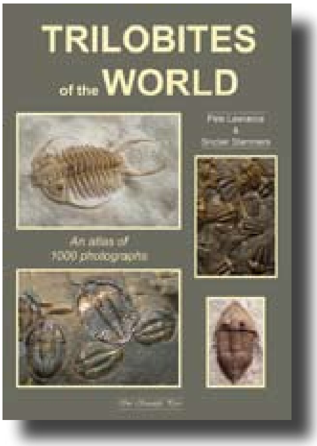

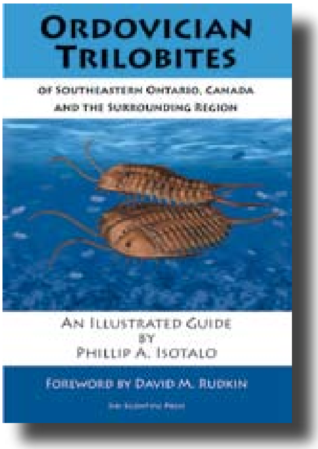
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OF SOUTHEASTERN ONTARIO, CANADA AND THE SURROUNDING REGION
AN ILLUSTRATED GUIDE
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